Hyoliths with pedicles illuminate the origin of the brachiopod body plan

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Abstract

Hyoliths are a taxonomically problematic group of Palaeozoic lophotrochozoans that are among the first shelly fossils to appear in the Cambrian period. On the basis of their distinctive exoskeleton, hyoliths have historically been classified as a separate phylum with possible affinities to the molluscs, sipunculans or lophophorates – but their precise phylogenetic position remains uncertain. Here we describe a new orthothecide hyolith from the Chengjiang Lagerstätte (Cambrian Series 2 Stage 3), *Pedunculotheca diania* Sun, Zhao et Zhu gen. et sp. nov., which exhibits a non-mineralized attachment structure that strikingly resembles the brachiopod pedicle – the first report of a peduncular organ in hyoliths. This organ establishes a sessile, suspension feeding ecology for these orthothecides, and – together with other characteristics (e.g., bilaterally symmetrical bivalve shell enclosing a filtration chamber and the differentiation of cardinal areas) – identifies hyoliths as stem-group brachiopods. Our phylogenetic analysis indicates that both hyoliths and crown brachiopods derived from a tommotiid grade, and that the pedicle has a single origin within the brachiopod total group.

Keywords: Pedicle, orthothecide hyoliths, phylogeny, stem brachiopod, Chengjiang Lagerstätte, Cambrian

1. Introduction

Hyoliths – orthothecides and hyolithides – are enigmatic Palaeozoic fossils known principally from their originally aragonitic [1] shelly elements, which comprise an elongate conical shell (‘conch’) capped with a lid-like operculum and, in the hyolithide subgroup, a pair of elongate ‘helens’ [2]. On account of this unfamiliar morphology, the ecology and relationships of this group have long attracted debate. A recurrent suggestion treats hyoliths as an extinct phylum in taxonomic limbo between molluscs and sipunculans [3], but recent reports of soft tissue anatomy [4] have led to the disputed [5, 6] suggestion that hyoliths belong to the brachiozoan group, which contains the brachiopod and phoronid phyla. However, their precise phylogenetic position remains obscure.

We report a new, exceptionally preserved orthothecide genus from the early Cambrian of China, which reveals taxonomically significant new details of the hyolith body plan. Phylogenetic analysis of a new morphological dataset that encompasses the major lophotrochozoan groups indicates that hyoliths are stem-group brachiopods, and addresses longstanding palaeontological problems concerning the origin of the brachiopod lineage.

2. Results

Superphylum Brachiozoa Cavalier-Smith, 1998

Stem-group of Phylum Brachiopoda Duméril, 1806

Class Hyolitha Marek, 1963

Order Orthothecida Marek, 1966

Remarks. Our specimens are attributed to Orthothecida (*sensu* [7]) based on the absence of a ligula and the absence of lateral sinuses (depressions of the commissure that accommodate the helens of hyolithides). Our material exhibits a highly compressed, subcircular cross-section, a pair of lateral furrows separating venter from dorsum, and one or two ventral grooves; as such, it cannot be accommodated in any existing orthothecide family. As the internal characters of the operculum and other essential features are not well preserved, we provisionally leave the family level taxonomy of this genus in open nomenclature.

***Pedunculotheca diania* Sun, Zhao et Zhu gen. et sp. nov.**

1996 *Ambrolinevitus* Sysoyev, 1985; Chen *et al.*, 1996, p. 139, fig. 173 [8]

2004 *Ambrolinevitus ventricosus* Qian, 1978; Chen 2004, p. 203, fig. 308 [9]

(Figures 1–3; Supplementary figures S1 and S2)

Etymology. *Pedunculotheca* refers to the peduncular attachment structure of the shell; *diania* reflects an abbreviation of Yunnan Province, from where the fossils were recovered.

Holotype. NIGPAS (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing) 166593 (figure 1*a*).

Additional material. Twenty-four further slabs (NIGPAS 166594–166617), bearing 44 conical shells and 17 opercula. Ten of the conical shells preserve incomplete attachment structures.

Occurrence. Cambrian Series 2 Stage 3, the Maotianshan Member of the Yu'anshan Formation (*Eoredlichia-Wutingaspis* Assemblage Zone), at sections near Yaoying Village in Wuding County, Shankou Village in Anning County, and Ma'anshan Village in Chengjiang County, Yunnan Province, China (see Supplementary table S1).

Preservation. The material exhibits Burgess Shale-type preservation of non-mineralized tissues [10] in the fashion typical of the Chengjiang deposits [11].

Terminology. Our description uses standard terminology (see [2, 12]), though we prefer the taxonomically neutral term 'conical shell' to 'conch' (following [4]).

Diagnosis. Orthothecide with slender, orthoconic, transversely ridged conical shell. Dorsum broadly rounded with a pair of lateral furrows, grading into broadly rounded

lateral margins. Venter similarly convex with one medial or two lateral furrows. Dorsoventral transition broadly rounded, producing a subcircular transverse section. Apex of conical valve bears rimmed subcircular disc in smaller specimens, regularly striated attachment structure with spinose terminal holdfast in larger specimens. Operculum circular to subcircular, bearing concentric growth lines, with bilobate bulge on exterior surface. Indistinct boundary between small cardinal shield and large conical shield on internal surface.

***Description*.** Complete specimens range from 6.2 to 25.5 mm long (mean: 14.7 mm; n = 15), 2.4 to 5.5 mm in apertural width (mean: 4.2 mm; n = 12), and 2.3 to 5.6 mm in opercular diameter (mean: 3.1 mm; n = 9). The ratio of apertural width to shell length ranges from 0.21 to 0.43 (mean: 0.31; n = 12). The operculum shows no ontogenetic variation: in all specimens it is circular (figure 2*d*) and covered by concentric lines (figure 1*a* and *c*). The opercular diameter is slightly smaller than the apertural width, indicating that the operculum could be retracted a short distance within the conical shell (figures 1*a*, 2*c* and *e*). The external surface of the operculum is convex close to the mediodorsal part, and features a bilaterally disposed pair of ridges that emerge from a raised quadrangular or oval area near the summit (figures 1*a*, *c* and 2*c*–*e*). Internally, a sharp change in convexity distinguishes the dorsal and lateral regions of the operculum (figure 2*d*), weakly delimiting a small cardinal shield from a large conical shield.

105 The apex of the conical shell bears a flat circular region around 0.7 mm across,
106 presumably corresponding to a metamorphic shell (*sensu* [13]). In small individuals,
107 the apices are flattened, with no obvious opening. The flattened surface is surrounded
108 by a prominent rim, rather than the recessed groove that would be expected if it
109 represented a septum [14]. In larger specimens, this region is replaced by a
110 non-biomineralized attachment structure, measuring 2.4 mm in length where it is
111 unambiguously complete (figure 1*a*). This stalk-like structure bears a central cavity
112 (figures 1*c*, *d*, 2*a* and *b*) and an external ornament of transverse striations whose
113 spacing and relief is consistent with the ridges that ornament the conical shell (figure
114 1*a* and *b*): the spacing on attachment structure is 35 to 46 µm (mean = 38 µm; n = 30);
115 on the shell, 33 to 57 µm (mean = 44 µm; n = 240). The structure terminates with a
116 broad holdfast disk, from which marginal spines emerge (figure 1*a* and *b*). In adult
117 specimens, the apical portion of the conical shell is triangular in dorsal profile, and
118 exhibits a larger divergence angle (52–73°; mean: 59°; n = 7) than the rest of the shell
119 (12–15°; mean: 13°; n = 9). Two smaller individuals without peduncular structures
120 (figure 2*f* and *g*) suggest that these juveniles were attached by an apical part of the
121 shell or an epithelium emerging from its apex. As the metamorphic shell is not present
122 in larger specimens, subsequent growth of the attachment structure through ontogeny
123 must have been accommodated by resorption or detachment of the apex, as in certain
124 hyoliths (e.g. [14]) and brachiopods (e.g. [15]).

Ecology. The *Pedunculotheca* attachment structure (figure 3) seems to have been used for anchorage, as indicated by its digitate holdfast. This implies a sessile habit, which is difficult to reconcile with the deposit feeding strategy typically reconstructed on the basis of a meandering, often infilled alimentary tract [16-18]. Meandering guts, however, are known from suspension feeders [19], so do not provide a decisive ecological signal. We therefore consider *Pedunculotheca*, like certain hyolithides [4, 16, 20], to have been a suspension feeder.

3. Affinity of hyoliths

The discovery of a peduncular structure in hyoliths is invaluable in resolving the affinity of this problematic group. Although attachment apparatuses are common and diverse in sedentary animals (e.g., [21]), a pedicle-like structure contributes to a suite of skeletal and anatomical structures that together indicate an affinity with brachiozoans.

To test this proposal and evaluate the evolutionary implications of our observations, we constructed a phylogenetic dataset of 54 Lophotrochozoan taxa, each scored for 225 morphological characters (Supplementary Information §1). Figure 4 depicts a consensus of trees recovered by parsimony analysis under equal and implied weights ($3 \leq k \leq 24$), after correcting for the impact of inapplicable data [22, 23], which

143 account for 18.5% of the non-ambiguous tokens. Details of tree search procedures,
144 and results of analysis under a Bayesian implementation of the Mk model [24, 25] and
145 the uncorrected Fitch algorithm [26], are provided in Supplementary Information §2–
146 4; the choice of method impinges on certain details of the analytical results, but does
147 not affect our main conclusions.

148 Our data indicate that hyoliths are monophyletic; brachiopods and hyoliths are
149 derived from a paraphyletic tommotiid grade [27, 28] (figure 4). Hyoliths are the
150 sister taxon to a clade containing the tommotiids *Micrina*, *Mickwitzia* and
151 *Heliomedusa*, plus the brachiopod crown group.

152 A sister-group relationship between hyoliths and crown-group brachiopods is
153 supported by characters including a bivalved shell arrangement enclosing a filtration
154 chamber (character 72) and the differentiation of cardinal areas (pseudointerareas)
155 (characters 92, 107). Hyoliths are excluded from the brachiopod crown group as they
156 lack a subset of brachiopod synapomorphies: impressions of an attachment structure
157 and setae on the larval shell; a low ventral interarea or pseudointerarea (secondarily
158 increased in lingulellotretids, acrotretids and some craniiforms) and a lophophore that
159 coils anteriad (rather than posteriad) [4].

160 This position of hyoliths close to the basal node of Brachiopoda, in the context of
161 outgroup taxa, resolves the polarity of certain characters within the brachiopod

lineage, clarifying the position of some otherwise enigmatic brachiopod groups [29]. We recognize paterinids, *Salanygolina*, chileids and kutorginates as successive stem groups to the rhynchonelliforms (figure 4). The weakly-mineralized lingulellotretid *Lingulosacculus*, interpreted as a link between phoronids and linguliforms [30], instead falls within a monophyletic Linguliformea. The agglutinated *Yuganotheca* [31] seemingly represents a tommotiid, and belongs to the brachiopod stem group (though this last result is contingent on the correct handling of inapplicable data, see Supplementary Information §3).

Deeper in the tree, the tommotiids *Eccentrotheca* and *Dailyatia* group with *Halkieria* as a grade within total-group brachiopods from which hyoliths and crown-group brachiopods were derived, in line with many previous proposals (e.g., [32, 33]). Bayesian and Fitch parsimony, perhaps influenced by their mishandling of inapplicable data [23], prefer trees that group these taxa closer to the molluscs; but under both interpretations, tommotiids are reconstructed as a paraphyletic grade from which hyoliths and brachiopods evolved.

Despite the excellent fossil record of brachiopods [29], a disparate array of hypotheses have been put forwards to explain the origin of the brachiopod body plan [28, 31, 33, 34]. Our new observations and phylogenetic framework shed light on the origins of fundamental morphological innovations in the brachiopod total group.

Firstly, it is most parsimonious to reconstruct a single origin of the brachiopod pedicle stem-wards of hyoliths and the attached tommotiid *Paterimitra* (Supplementary Information §5.5). This corroborates the homology between the *Pedunculotheca* attachment structure and the brachiopod pedicle, indicating a primitively attached rather than vagrant ancestry of the brachiozoan lineage (cf. [35]).

It has been argued that the pedicles of linguliforms and rhynchonelliforms are not homologous [36-38], in part because they are secreted by different parts of the organism (the ventral mantle in linguliforms [39]; a larval pedicle lobe in living rhynchonelliforms [40]). Our results instead imply a stepwise transformation from an ancestrally linguliform-like pedicle to the derived state of extant rhynchonelliforms: the pedicle migrated from the hinge to the umbo in early-diverging *Salanygolina* [15] and chileids [41] (character 120), but retained its coelomic cavity (character 32) until the kutorginates had diverged. On this basis, we interpret the two pedicle openings in *Nisusia* [36] as representing an ontogenetic relocation of the pedicle.

The migration of pedicle to the apex of the ventral valve occurred independently in the linguliforms, by the enrolling of the delthyrium [42] (character 113); and again in *Pedunculotheca*. It is more parsimonious to accommodate this variation as modification to an existing pedicle than to infer multiple separate origins of this organ.

Secondly, our results illuminate the high variability of shell mineralogy within the brachiopods (character 128), which are conventionally subdivided based on the composition of the shell, i.e. phosphatic Linguliformea and calcareous Rhynchonelliformea or Craniiformea [43]. Our results show that this emphasis on mineralogy over morphology has led to the mis-classification of the phosphatic paterinids – which are not linguliforms, but early-diverging rhynchonelliforms that inherited a phosphatic mineralogy from the brachiopod common ancestor – and the calcitic *Mummpikia*, which is not a rhynchonelliform but an independently calcifying linguliform, as its morphology suggests [44] (figure 4). To this list we add three further instances of mineralogical modification: hyoliths represent an independent innovation of an aragonitic mineralogy, as do the trimerellids; and craniiforms obtained their calcitic shells independently from the rhynchonelliforms (as proposed by [44]) , from a trimerellid precursor. In sum, brachiopods subvert the general expectation that lineages rarely modify their mineralogy [45, 46].

Taking this further, our results show that shell microstructure is highly variable within the brachiopod total group. In particular, the ‘canaliculate’ microstructure (character 137) [1, 44, 47, 48] that has been afforded great importance – even to the point of identifying the Ediacaran reef-dweller *Namacalathus* [49] as a brachiozoan – turns out to have multiple origins across the brachiozoan total group, as do the broader ‘punctae’ (character 138). Hyoliths have been argued to have a mollusc-like

mineralogy and microstructure [6]. We contend that these variable characteristics are easily reconciled with a brachiopod affinity, and need not arise through common ancestry with molluscs – a group that have no obvious analogue for hyolith traits such as the pedicle, lophophore, or paired bilaterally symmetrical shells, and whose distinctive synapomorphies – a radula and creeping foot – have not been identified in even the best-preserved hyoliths.

Identifying hyoliths as stem-group brachiopods also resolves character polarity within the group itself. Moysiuk *et al.* [4] regarded hyolithides as primitive within Hyolitha, speculatively equating helens with tommotiid sclerites. We instead identify *Pedunculotheca* as primitive within Hyolitha (figure 4), on the basis of its retained brachiopod-like features. Hyolithides and other orthothecides are united by the secondary loss of a pedicle (character 26) and the morphology of their metamorphic shell (character 2) [2, 50-53], whose small fusiform to globular aspect differs from the discoidal shape of the larval shells of *Pedunculotheca* and Cambrian brachiopods [54].

The recognition of hyoliths as stem brachiopods indicates a profound change in the character of the group at the close of the Cambrian period. Early in the Cambrian, the brachiopod lineage was dominated by tommotiids, linguliforms and hyoliths: taxa with a high metabolic overhead, reflected by the extensive gut and relatively high volume of metabolically active tissue [4, 55-57], the use of phosphate as a biomineral

240 [58], and in certain tommotiids, an apparently vagrant ecology [32]. The end of the
241 Cambrian period witnessed a marked decline in these groups (Supplementary
242 figure S3), with a corresponding explosion in the taxonomic diversity of anatomically
243 modern crown-group brachiopods – in particular the rhynchonelliforms, whose
244 narrow disparity [55] reflects a fundamentally distinct ecological strategy, with a
245 hyper-efficient physiology adapting the lineage to nutrient-limited settings [59]. From
246 this perspective, the decline in hyolith diversity after their mid-Cambrian zenith
247 mirrors a broader decline in high-metabolism stem-group brachiopods, and their
248 supplanting in less nutrient-rich environments by their rhynchonelliform counterparts.

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250 Ethics. No special permissions were required for the collection of samples.

251 Data accessibility. Supplementary figures and tables, including details of phylogenetic
252 analysis and results, are provided at
253 https://web.archive.org/web/ms609.github.io/hyoliths/; source code is available at
254 https://github.com/ms609/hyoliths.

255 Phylogenetic data is accessioned with MorphoBank, project number 2800:
256 http://morphobank.org/permalink/?P2800

257 Authors' contributions. H.S., F.Z. and M.Z. designed the research and M.Z. and F.Z.
258 provided material; H.S., M.R.S. and H.Z. performed the research; M.R.S., H.S. and

G.L. contributed to the phylogenetic dataset; M.R.S. performed the phylogenetic analysis with input of H.S.; H.S. wrote the original draft; M.R.S. and H.S. revised and finalized the manuscript; all co-authors jointed the research and contributed to discussions.

Competing interests. The authors declare no competing interests.

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440

441 **Figure 1.** *Pedunculotheca diania* Sun, Zhao et Zhu gen. et sp. nov. from the

442 Chengjiang Biota, Yunnan Province, China. Fossil images in the bottom row

443 correspond to their interpretive drawings in the top row. (*a*) NIGPAS 166593,
444 holotype, complete specimen with operculum and attachment structure with terminal
445 holdfast; detail of boxed region shown in (*b*). (*c*) NIGPAS 166594, dorsoventrally
446 compacted specimen with operculum and partial pedicle structure. Detail of boxed
447 region shown in (*d*). Scale bar = 2 mm. Abbreviations: cc = coelomic cavity, co =
448 conical shell, da = dorsal apex, do = dorsum, ho = holdfast, op = operculum, sp =
449 spine, ve = venter.

450

451 **Figure 2.** *Pedunculotheca diania* Sun, Zhao et Zhu gen. et sp. nov. from the
452 Chengjiang Biota, Yunnan Province, China. (*a*) NIGPAS 166595, shell with
453 incomplete pedicle structure with coelomic cavity. Detail of boxed region shown in
454 (*b*). (*c*) NIGPAS 166599a, juvenile conical shell with operculum showing two
455 longitudinal ventral grooves and circular larval shell. (*d*) NIGPAS 166598, interior of
456 external mould of operculum displaying circular outline. (*e*) NIGPAS 166597, a
457 conical shell preserved operculum and soft parts, showing a compressed elliptic cross-
458 section. (*f*) NIGPAS 166600, juveniles showing intact larval shells and two or one
459 central longitudinal grooves; detail of box shown in (*g*). Scale bars = 2mm for (*a*, *c*, *e*
460 and *f*) and 1mm for (*b*, *d* and *g*). Abbreviations: cc = coelomic cavity, da = dorsal apex,
461 pe = pedicle.

462

463 **Figure 3.** Artistic reconstruction of *Pedunculotheca diania* Sun, Zhao et Zhu gen. et
464 sp. nov. Adult specimen shown in feeding position.

465

466 **Figure 4.** Majority rule consensus of all trees that are optimal under parsimony
467 analysis using equal or implied weights ($3 \leqslant k \leqslant 24$), indicating key evolutionary
468 transitions. Node labels denote frequency in optimal trees (first figure) and posterior
469 probability under Bayesian analysis (second figure). For details, see Supplementary
470 information.